PAN-PACIFIC ENTOMOLOGIST
October 1979, Vol. 55, No. 4, pp. 261–266

LIFE HISTORY OF *ZYGOGRAMMA TORTUOSA* ROGERS ON THE RAGWEED, *AMBROSIA ERIOCENTRA* (GRAY) PAYNE, IN SOUTHERN CALIFORNIA (COLEOPTERA: CHRYSOMELIDAE)

R. D. Goeden and D. W. Ricker

Dept. of Entomology, Univ. of California, Riverside 92521

Zygogramma tortuosa is one of several stenophagous species of phytophagous insects associated with the native perennial ragweed, *Ambrosia eriocentra,* in southern California (Goeden and Ricker, 1976b). This leaf beetle was exported by us to the U.S.S.R. in 1976 for quarantine study by Dr. O. V. Kovalev, All-Union Institute of Biological Control, Kishinev, Moldavia, U.S.S.R., as a candidate agent for the biological control of ragweeds (Goeden et al., 1974). Unfortunately, the adults defoliated sunflower, *Helianthus annuus* L., an important cultivar in Eurasia, in laboratory feeding tests; consequently, the colony of *Z. tortuosa* was destroyed and no use was made of this natural enemy in ragweed control in the U.S.S.R. (O. V. Kovalev, pers. commun.).

We herein describe our ancillary, field, insectary, and laboratory findings on the life history of this heretofore little-known leaf beetle. Insectary conditions were 27 ± 1°C, 40–70% relative humidity, and a 12/12-hr (light/dark) photoperiod.

Distribution and host plant.—Linell (1896) gave the range of *Z. tortuosa* as Arizona and New Mexico. We studied field populations at the following Mojave Desert locations in northeastern San Bernardino Co.: Cedar Canyon, Hackberry Mountain, and Mountain Pass. In southern California, these beetles, like their host plant, are largely confined to sandy or gravelly washes at ca. 800–1600 m elevations in or near the following types of plant communities described in Munz (1974): Creosote Bush Scrub, Joshua Tree Woodland, and Pinyon-Juniper Woodland.

Our faunistic studies of ragweeds in southern California indicated that *Z. tortuosa* is a true monophage, whose only natural host plant is *A. eriocentra* (Goeden and Ricker, 1976b). In the insectary, *Z. tortuosa* additionally has been reared from egg to adult on potted specimens of *Ambrosia chenopodiifolia* (Bentham) Payne, *A. confertiflora* Decandolle, *A. dumosa* (Gray) Payne, *A. ilicifolia* (Gray) Payne, *A. psilostachya* Decandolle, and *A. pumila* (Nuttall) Gray. None of these ragweeds is attacked by *Z. tortuosa* in nature (Goeden and Ricker, 1975, 1976a, 1976c).

Biology.—*Egg*.—The egg (Fig. 1a) is oblong and yellow-orange to salmon pink. The chorion is sub-lustrous and finely and regularly punctate. Fifty

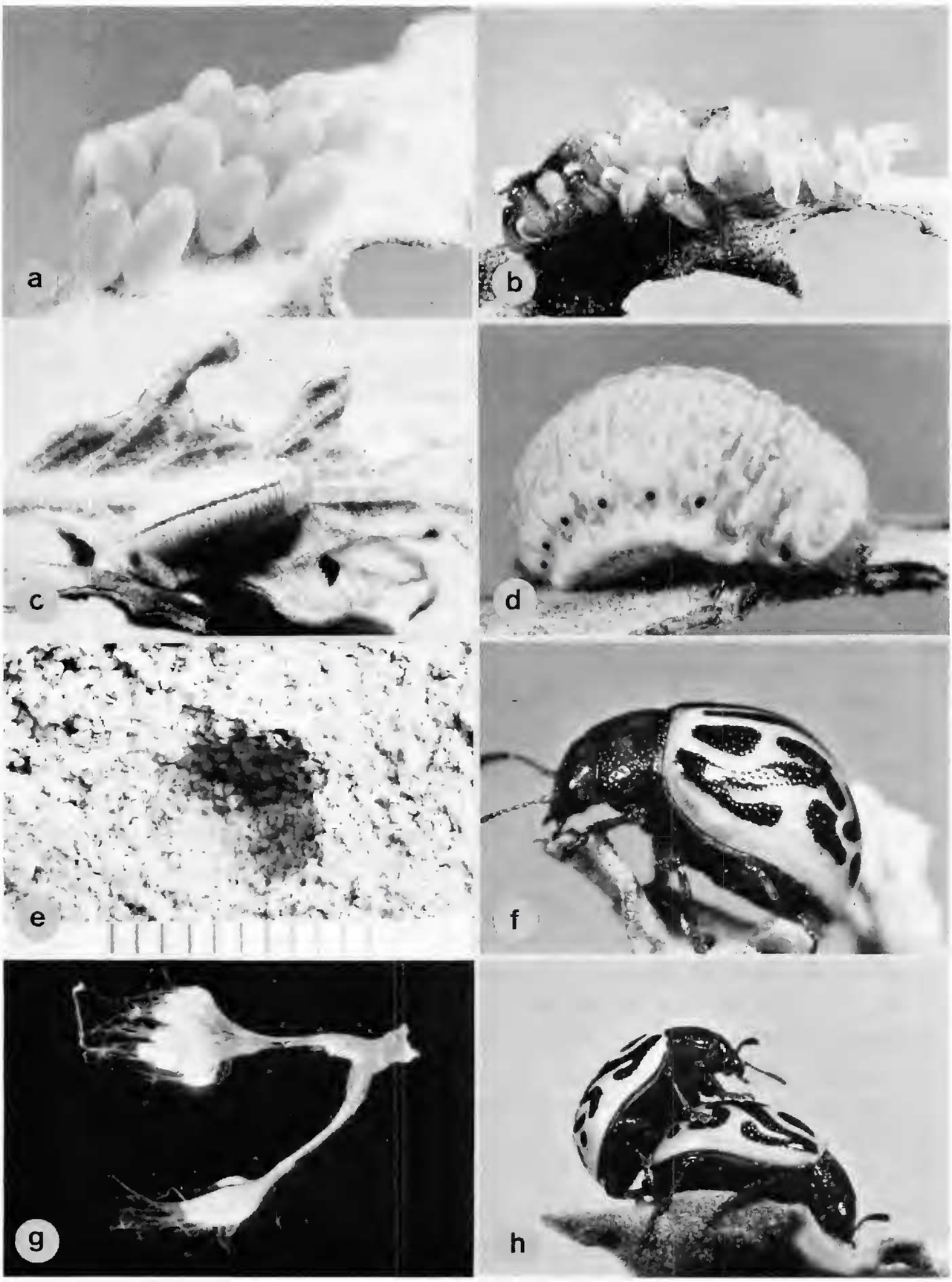

Fig. 1. Life stages of *Zygogramma tortuosa*. (a) egg mass, 10×, (b) newly hatched larvae, 5×, (c) third instar and feeding damage on leaf of *Ambrosia eriocentra*, 5×, (d) mature, fourth instar, 7×, (e) pupal cell, rule divided into mm, (f) adult female, 6×, (g) immature ovaries of newly emerged female, 10×, (h) adults *in copula*, 4×.

eggs averaged (±S.D.) 1.36 ± 0.05 mm in length and 0.60 ± 0.03 mm in greatest width.

In the field, eggs usually were laid on end at an angle in elongate clusters along the midribs on the undersides of the distal halves of the laminae of the younger, more apical leaves (Fig. 1a). Mature leaves also bore eggs. Each egg was firmly affixed with a clear, mucilaginous secretion to the leaf surface. An average of 7.9 ± 3.7 (range: 2–21) eggs were counted in 139 clusters examined in the field. Only 2 (0.2%) of 1083 eggs examined were laid singly. The incubation period was 3–4 days under insectary conditions.

Larva.—There are four instars. The larvae are cyphosomatic, slightly C-shaped, and legged. They generally are sluggish in their locomotion, which is aided by abdominal terminalia modified as a protrusible "proleg." Their general body color is yellowish-white and is derived from the copious fatty tissue that accumulates beneath the thin, semi-transparent, unsclerotized integument of the thorax and abdomen. The head capsule is dark yellow. The antennae, legs, mouthparts, and spiracles are more heavily sclerotized and darkened. The head capsule widths of 15 each, first–fourth instars averaged: 0.55 ± 0.004 mm, 0.80 ± 0.010 mm, 1.16 ± 0.017 mm, and 1.55 ± 0.014 mm, respectively.

Larvae hatched concurrently from the same egg mass (Fig. 1b). The newly eclosed larvae rested on or near their discarded chorions until their exoskeletons hardened. They then moved to and immediately began to feed, at first somewhat gregariously, on the younger, terminal foliage. Second instars began to feed as scattered individuals. Older larvae solitarily fed on the margins of the blades of both young and old leaves. Irregular, slightly ragged, elongate incisions were made along the leaf margins, though the midribs usually remained uneaten (Fig. 1c). Larval feeding also was evidenced by the brownish-black, stringy feces that littered attacked foliage. In nature, individual plants rarely were severly defoliated, because field populations of *Z. tortuosa* seldom were high and feeding was dispersed.

In isolated insectary rearings on bouquets of fresh branch terminals of *A. eriocentra,* larval development by 15 individuals lasted 20 ± 3 (range: 13–22) days. An average of 8 ± 3 (range: 1–11) days (ca. 40%) of the last part of this period was spent at rest on a leaf as a nonfeeding, fourth instar. The first larval stadium lasted 2–3 days; the second stadium, 1–2 days; the third stadium, 1–5 days; and the fourth stadium, 5–17 days. The larvae grew in length from 1.5–2.5 mm as first instars to 4–6.5 mm as fourth instars. Moulting usually occurred on leaves. The mature larvae (Fig. 1d) became positively geotactic and crawled or dropped to the ground and tunneled into the soil.

Pupa.—No pupae were observed in nature. In moist, sandy, potting soil in cagings in the insectary, 24 prepupae formed spherical pupal cells of compacted, not glued, soil particles (Fig. 1e) that measured 6.1 ± 0.8 (range:

4.6–7.8) mm in diameter. The pupal stadium lasted 4–5 days. An additional 4–5 days were spend hidden in the soil, first as prepupae, then as newly formed, fully sclerotized and pigmented adults.

Adult.—The adult (Fig. 1f) is an attractive, ferrugineous beetle with pearly white and black-patterned elytra. The posterior margin of the fifth abdominal sternite is weakly trilobed in the male, smoothly rounded in the female. Both sexes emerged concurrently and in approximately equal numbers from insectary rearings (1:1.4, females:males, n = 223). Newly emerged females did not mate and were sexually immature (Fig. 1g). In nature, these new adults emerge and feed actively on leaves for 1–2 weeks, then scatter, and bury themselves at unknown depths, presumably in the sandy soil of the desert washes containing their host plants.

After feeding on the foliage of potted *A. eriocentra* in the insectary, 74 newly formed beetles buried themselves separately in the potting soil at a mean depth of 35 ± 12.7 (range: 5–60) mm. Females dug from the soil showed no oogenesis upon dissection (Fig. 1g). Twenty pairs (1 male, 1 female) of newly formed beetles also were held in the insectary in separate cages provided with bouquets of fresh *A. psilostachya* foilage, renewed weekly, but no soil as a hibernation medium. Under these conditions, 19 males lived an average of 106 ± 40 (range: 36–172) weeks; 16 females, 131 ± 50 (range: 34–197) weeks. These data exclude beetles that died accidentally or escaped. At intervals of 1–10 months, the survivors resumed feeding for 1 to several weeks and then became inactive again.

In mid-January, 1974, we carefully excavated ca. ¼ m^3 of loose sand and gravel to a depth of ca. 20 cm from beneath an isolated clump of *A. eriocentra* at the Hackberry Mountain site that had borne many larvae and adults the previous fall. Only 1 dead, but intact beetle was found at a depth of 43 mm, indicating that the beetles scattered and did not concentrate beneath their host plants for hibernation. Diapausing in scattered locations serves to spread the risk of accidental death in their unstable, harsh environment, which is subject to flash flooding and severe erosion following moderate to heavy, seasonal rainfall.

Sixteen, overwintered, feeding and mating females field-collected from plants on July 25, 1974, before oviposition had begun, were caged separately, each with a male and a bouquet of *A. eriocentra* (renewed daily), in the insectary. The beetles laid 145 ± 67 (range: 21–242) eggs during a 10.5 ± 2.6 (range: 7–18)-day oviposition period. Based only on days when females oviposited, they laid 15.8 ± 11.9 (range: 1–48) eggs daily. These females were observed *in copula* (Fig. 1h) an average of 3 (range: 0–7) times and lived an average of 2 (range: 0–12) days after they ceased oviposition.

Beetle flight only was observed once in the field. Here, a beetle crawled to the apex of a vertical branch at mid-day on September 3, 1975, and took flight in still air. It flew over 2 large *A. eriocentra* at ca. 1-m height, up the

wash, and out of sight. Most beetles observed in the field during the day were individuals at rest in sun or shade on leaves and stems, where copulation also occurred (Fig. 1h).

Host specificity.—Forty, newly hatched larvae were individually transferred with a fine, camel hair brush to the leaves of each of 6, potted ca. 30-cm tall, vegetative, sunflower shoots in ventilated, glass-topped, 34 × 32 × 35-cm, sleeve cages in the insectary. All but 4 of the larvae died as first instars, and the survivors died as new second instars after they had vacated the plant. Sixteen (40%) of 40 larvae similarly transferred as a check to a potted *A. eriocentra* subsequently were recovered as adults. Therefore, it is doubtful that *Z. tortuosa* would have reproduced on sunflowers in Russia.

Both overwintered, sexually mature beetles and newly emerged, immature adults fed readily on leaves of bouquets of sunflower shoots in the insectary (3 replicates of 8 beetles each). As a further test, 150, 100, and 100 overwintered, field-collected, sexually mature beetles were individually transferred on 3 separate days, respectively, in August, 1977, to leaves of 6 sunflower plants (81–112 cm in height) grown in a 1.1-m row out-of-doors at Riverside. After 1 or 2 days in all 3 trials, no beetles remained on these plants; moreover, no feeding or oviposition by *Z. tortuosa* occurred. Therefore, it is questionable whether *Z. tortuosa* would have attacked sunflower if released in the field in Russia. However, the induced feeding obtained there on sunflower in the laboratory caused sufficient concern to reject this beetle as a biological control agent.

Seasonal history.—Beetle emergence, feeding, and maturation is triggered by mid-summer/early-fall rainfall sufficient to cause water flow in the desert washes. This activity occurs regardless of the condition of the *A. eriocentra* present, i.e., abundant host-plant foliage generated by ample winter moisture will be unexploited if no mid-summer/early-fall rainfall stimulates beetle emergence and reproduction. Similarly, if rainfall is too light, beetle emergence may be limited, and oviposition also limited or absent, again, even in the presence of abundant host-plant foliage. If no rainfall occurs or no water flows from higher areas receiving rain in a wash containing diapausing beetles, they presumably remain underground for an additional year. Judging from their insectary longevity and observed field behavior, their diapause may extend for 2 or 3 (possibly more) years under extreme drought conditions.

Zygogramma tortuosa is univoltine, at best, in southern California. Beetle emergence, mating, and initial oviposition were observed in late-July through September, 1971–72, 1974–78, at those study sites where detectable rainfall and water run-off had occurred during the previous 1–2 weeks. Larvae and F_1 beetles were present in early-August through mid-October.

Mortality factors.—No parasites were reared from egg masses collected in the field. Larvae and adults of *Z. tortuosa* accidentally cannibalized eggs.

Egg predation by adults of *Hippodamia convergens* Guerin (Coleoptera: Coccinellidae) was observed repeatedly. Moreover, *Nabis americoferus* Carayon (Hemiptera-Heteroptera: Nabidae) was a suspected egg predator as well as a confirmed predator on young larvae. An adult of *Sinea confusa* Caudell (Hemiptera-Heteroptera: Reduviidae) was observed preying on an adult *Z. tortuosa*. *Doryphorophaga doryphorae* (Riley) (Diptera: Tachinidae) was reared from a prepupae collected as an early instar in the field.

Acknowledgments

Zygogramma tortuosa was identified by Dr. R. E. White, Systematic Entomology Laboratory, IIBIII, USDA, % U.S. National Museum of Natural History, Washington, D.C. The entomophagous insects were identified by Drs. R. D. Gordon, J. L. Herring, and C. W. Sabrosky, same address.

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